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Breeding behaviour of larks in the Kalahari Sandveld

by

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SYNOPSIS

There are eight species of larks (Alaudidae) breeding in the southern part of the Kalahari Gemsbok National Park; they belong to the genera *Mirafra* (three spp.), *Chersomanes* (one sp.), *Eremopterix* (two spp.), *Spizocorys* (one sp.) and *Alauda* (one sp.). Each species has its own characteristic song, usually associated with a song-flight over the territory. The nest in most, if not all, species is built by the female alone, usually within four to seven days. Eggs are laid at 24-hour intervals. To judge from the difference between mean egg measurements in summer and in winter, it is possible that two different subspecies of *Eremopterix verticalis* breed at different times in the Gemsbok Park. Incubation takes 12 days in all species and the chicks leave the nest at about 10 days, well before they can fly. Chicks are led away from the nest by the female parent, although both parents feed the chicks. In the genus *Eremopterix* both parents incubate the eggs. All species of sandveld larks have characteristic alarm- and intruder-reactions at the nest; some of them have distraction displays of the injury-feigning type, others apparently do not.

INTRODUCTION

Certain aspects of the breeding biology of the Kalahari larks have already been dealt with in papers on lark ecology (Maclean, in press) and systematics (Maclean, 1969). These two papers also constituted in some measure a review of lark literature, not only for southern Africa, but also for the entire range of the family Alaudidae. The present work is concerned primarily with the behavioural aspects of lark breeding biology.

There are eight breeding species of larks in the Kalahari Gemsbok National Park where this study was done:

1. Fawn-coloured Lark *Mirafra africanoides*
2. Clapper Lark *M. apiata*
3. Sabota Lark *M. sabota*
4. Spike-heeled Lark *Chersomanes albofasciata*
5. Grey-backed Finch-lark *Eremopterix verticalis*
6. Black Finch-lark *E. australis*
7. Pink-billed Lark *Spizocorys conirostris*
8. Stark's Lark *Alauda starki.*

The study lasted from October 1964 to April 1966.

SONGS AND SONG-FLIGHTS

Although the songs and accompanying flight displays of most of the sandveld larks were described to some extent in an earlier work (Maclean, 1969), a more detailed account will be given here, since general texts on southern African birds (e.g. Mackworth-Praed & Grant, 1962; McLachlan & Liversidge, 1957) give only the most cursory descriptions.

1. *Mirafra africanoides*

The song of the Fawn-coloured Lark is usually uttered from a perch or in flight, but may even be uttered on the ground. The song is a jumbled series of notes difficult to transcribe: it begins with four or five deliberate staccato notes, passes into a rapid phrase and usually ends in a single descending and somewhat drawn-out note thus: 'chip chip chiree chip chiree chiree chiree chweeeer'. The final long note may not always be present. The same song is uttered by both sexes.

During the song-flight the bird cruises at a height of about 20 to 30 metres or more above the ground. The wing-beats are rather exaggerated, although the bird tends not to move much relative to the ground. As each song phrase is uttered, the wings are held stiffly out and the bird goes into a shallow dive; as soon as the song phrase ends, the fluttering cruising flight is resumed. Each phrase lasts about four or five seconds and the phrases occur from seven to ten seconds apart. A whole song-flight may last for several minutes at a time.

2. *Mirafra apiata*

The song-flight of the Clapper Lark takes two forms. The more usual form is an aerial cruise at a height of 20 to 30 metres, during which the bird flutters along, then rises with exaggeratedly flapping wings. Towards the top of this climb, the wing-clapping (a loud rattling like distant machine-gun fire) is produced. At the top of the climb the wings are held stiffly out at a high dihedral and the bird drops several metres in a steep dive as it utters its plaintive rising whistle, a single long note. Then the fluttering flight is resumed before the next climb, clap and whistled dive. Each of these sequences is performed at intervals of about 15 to 30 seconds and a whole song-flight may last for more than ten minutes.

Less commonly the bird performs a similar display from a perch or from the ground. It takes off and rises with steep fluttering flight to a height of some ten metres, clapping the wings at the top of the climb, then descends with the steep whistled dive, which may take it straight down to the ground or may end in normal flight either to a perch or to the ground. Whether or not both sexes do this display was not determined.

3. *Mirafra sabota*

The description by McLachlan & Liversidge (1957) of the song of the Sabota Lark—'a weak song of a few notes'—is misleading. The song may in fact be quite loud and penetrating, but difficult to transcribe. The phrase is short and varies considerably from one individual to another; it is rather canary-like at times and is almost invariably uttered from a perch on top of a bush or tree. One song phrase that I have heard from at least two different birds is a loud and far-reaching 'pip pip *peeu*' uttered repeatedly at intervals of a few seconds; the first two notes are sharp and high pitched, the last note briefly drawn out and descending in pitch.

Sabota Larks are accomplished imitators of other birds. In the Gemsbok Park I have heard them imitate the following species: *Rhinoptilus africanus*, *Certhilauda albofasciata*, *Bradornis infuscatus*, *Malcorus pectoralis*, *Cercomela familiaris*, *Sporopipes squamifrons* and *Passer melanurus*. In South West Africa just west of the Kuiseb River in Game Reserve No. 3 I have heard the Sabota Lark imitate *Rhinoptilus africanus*, *Mirafra curvirostris*, *Cercomela schlegelii* and *Onychognathus nabouroup*.

4. *Chersomanes albofasciata*

The variety of vocalizations in the Spike-heeled Lark seems to be limited to variations on a basic trilling 'tree' note with a slight nasal quality. There is a rapid 'tree-tree-tree-tree' phrase, uttered from the ground or from a low perch on a bush, that I have tentatively construed as a song, although the notes are very similar to the commonly heard flight-call. The 'song' is, however, somewhat higher pitched; it may start off with two or three deliberate notes before running into the burst of quick notes already described. The behaviour of the Spike-heeled Lark has been inadequately studied and I should emphasize the tentative nature of any interpretations I may make regarding its behaviour in this paper.

5. *Eremopterix verticalis*

The song-flight of the Grey-backed Finch-lark consists in flying about the territory in large circles a few metres above the ground, often with the legs dangling. The song is pleasant, but simple and unmelodious, sounding like 'twip twip chik' repeated over and over again. The flight does not end in a vertical drop as in some larks.

6. *Eremopterix australis*

The Black Finch-lark has a song-flight essentially similar to that of *E. verticalis*, but without the hanging legs. The song is quite different, consisting of buzzy notes, although I have also recorded a short, canary-like song from a male on the ground. The song-flight resembles the 'butterfly' flight of some Fringillidae and is accentuated by the broad black wings.

7. *Spizocorys conirostris*

The song of the Pink-billed Lark seems to be similar to the flight-call. I have, however, also recorded a very faint series of notes from a bird sitting on the ground about four to five metres away, that sounded like the stridulation of some insect, 'trrr krik krik'. The significance of these notes is obscure, but they may represent the audible components of a song, most of which is too high-pitched for the human ear to hear.

8. *Alauda starki*

In an earlier work (Maclean, 1969) I described the song and song-flight of Stark's Lark as follows: 'It rises singing a simple, mellow song "prrr prrr preee preee prrr prrr preee preee", etc. until it gets to a height of about 20 or 30 feet where it continues to sing in one place for a short while before dropping straight down to the ground. The final drop is done in silence.' I also noted that the song may be uttered from a perch on a low shrub.

NEST BUILDING

Nest architecture in the sandveld larks has already been dealt with in detail (Maclean, in press). The construction of the nest in the two *Eremopterix* species is done entirely by the female, but I was unable to determine whether or not the male helps her with the initial excavation. He probably does not, although he accompanies the female on her trips to collect nesting material. This seems to be the normal pattern of nest-building behaviour in larks, as it has been found also in those species that are not sexually dichromatic, e.g. *Lullula arborea* (Koffán, 1960; Labitte, 1958; Wadewitz, 1957), *Galerida cristata* and *G. theklae* (Abs, 1963), *Eremophila alpestris* (Pickwell, 1931) and *Alauda arvensis* (Lebeurier & Rapine, 1935). Koffán (1960) noted that the male of *Lullula arborea* may carry nest material and may help the female with the shaping of the nest cup, but does not do any proper building.

The only nest material that I have seen brought to the nest by the male of any sandveld lark is a mixture of sand and spider web in the case of *Eremopterix australis*. The male drops the blob of sandy web into the nest cup when he comes to relieve the female during incubation; he then sits on both the eggs and the web. When the female returns to incubate, she picks up the blob of sandy web, places it on the rim of the nest and smooths it flat. All the nests of *E. australis* in the sandveld were thus decorated with a rim of sandy web. A very few nests of other species also had this material on the rim, but never in the same quantity. For instance only 3 out of 39 nests of *Chersomanes albofasciata*, 1 out of 58 nests of *Spizocorys conirostris* and 4 out of 6 nests of *Alauda starki* were thus decorated. In addition to this, the nest of *Spizocorys conirostris* had some tubular casings from harvester termite (*Hodotermes*) tunnels on the rim. I was unable to determine which sex brought the decorative material in the case of these other species.

The time taken to build a nest was difficult to assess. It was not easy to find nest scrapes in the first stages of excavation and desertion of incomplete nests was so common as almost to constitute a rule. However, estimates give the following approximate figures for the time lapse between the start of excavation and the completion of the nest cup: *Chersomanes albofasciata*, four to seven days; *Eremopterix australis*, four to five days; *Spizocorys conirostris*, just over four days. The time taken to construct the cup alone was between two and five days in all the species studied, except for the three *Mirafra* species in which estimates were not possible. These times seem on the whole rather shorter than the times of two to sixteen days in *Eremophila alpestris* (DuBois, 1935) and eight days in *Alauda arvensis* (Lebeurier & Rapine, 1935), but compare with the two to four days for *Eremophila alpestris* given by Pickwell (1931).

Once the excavation is complete, the first pieces of foundation material (sticks, clods, stones) are laid around it (fig. 1). A foundation is not always present (Maclean, in press). The nest cup is made of finer materials, usually dry grass, dropped into the excavation by the female and shaped by pressing it downwards and outwards with her body.

The female may continue to bring nest material even after the clutch is complete and incubation has begun (fig. 2). This has also been noted in *Eremopterix leucotis* (Steyn, 1964). Once an incubating male *E. australis* was seen pecking at the nest material, but this was a nervous response to the close proximity of a motor vehicle. This behaviour may, however, indicate that nest building has been lost only relatively recently in male larks.

EGG-LAYING AND INCUBATION

In all the species studied, successive eggs in a clutch were laid at about 24-hour intervals. Clutch size in the sandveld larks has already been treated in detail (Maclean, in press).

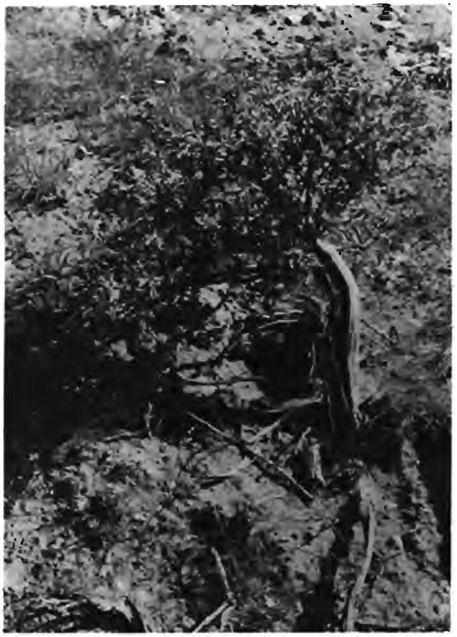

Fig. 1. The nest excavation of *Eremopterix australis* under a small shrub, with the first pieces of foundation material lying around the scrape.

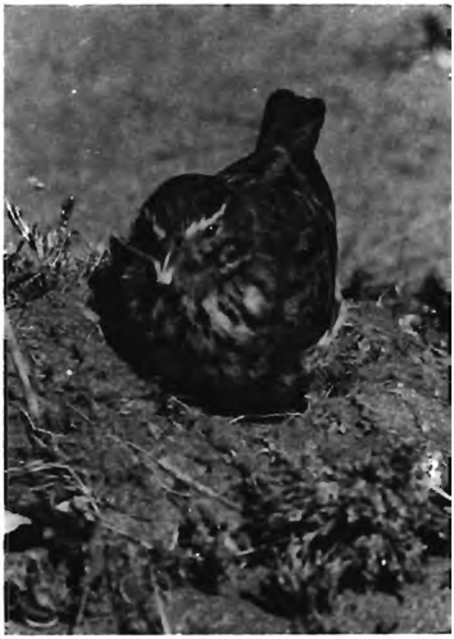

Fig. 2. A female *Eremopterix australis* brings nest material as she returns to incubate her two eggs.

Egg measurements appear in Table 1. The means for all species add little new to our knowledge of lark eggs in South Africa, except in the cases of *Eremopterix australis* and *Alauda starki* for which previous information was obtained from a single clutch (McLachlan & Liversidge, 1957).

While analysing egg measurements for *Eremopterix verticalis*, I noticed a trend towards smaller eggs in summer than in winter. The differences were analysed statistically and found to be highly significant (Table 2). The differences between summer and winter means for the eggs of *Chersomanes albofasciata* and *Eremopterix australis* were, however, not statistically significant (Table 2).

Ten clutches of *E. verticalis* in which the first and second eggs were known gave means for the first egg of 19·4 × 13·9 mm and for the second egg of 19·3 × 14·1 mm. In seven of the ten cases the second egg was shorter than the first and in six cases the second egg was broader than the first; these differences may prove to be significant when larger samples have been obtained.

Incubation in *E. verticalis* almost invariably starts with the first egg. The same appears to be true of *E. australis* and *Spizocorys conirostris*. *Chersomanes albofasciata* may or may not start incubating before the clutch is complete. Hatching in a clutch of *Mirafra africanoides* is usually synchronous, so it may normally complete the clutch before starting incubation; direct information on this and the other *Mirafra* species and on *Alauda starki* is lacking.

TABLE 1

Species	Egg measurements (mm)									
	Length					Diameter				
	Max.	Min.	Mean	N	S.D.	Max.	Min.	Mean	N	S.D.
M. africanoides ..	23·4	17·2	20·8	24	1·257	15·6	11·9	14·8	24	0·767
M. sabota ..	20·7	20·4	20·6	3	—	15·1	14·9	15·0	3	—
C. albofasciata ..	22·5	19·3	20·9	64	0·938	16·3	13·7	14·9	64	0·500
E. verticalis ..	20·6	16·9	19·3	267	0·787	15·1	12·3	13·9	267	0·476
E. australis ..	20·6	16·7	18·3	101	0·838	14·9	12·3	13·4	101	0·489
S. conirostris ..	24·6	17·3	18·7	92	1·002	14·2	11·8	13·7	92	0·539
A. starki ..	20·4	19·0	19·7	12	0·420	14·8	13·4	14·3	12	0·421

Egg measurements of Kalahari sandveld larks for all seasons. N = sample number. S.D. = standard deviation. S.D. for *M. sabota* has been omitted because of too small a sample.

In both *Eremopterix* species both sexes incubate the eggs (figs. 2 and 3). Insufficient time was spent at the nests of other species to observe nest-relief and, since the sexes are alike, it is not possible to say whether or not both sexes incubate. There seems to be no general rule about this in the Alaudidae. For instance, incubation by the female only is found in *Eremophila alpestris* (DuBois, 1935; Fobrush, 1927), *Galerida cristata* (Abs, 1963; Hartley, 1946) and *G. theklae* (Abs, 1963), whereas both sexes incubate in *Mirafra javanica* (Bourke, 1947) and *Eremopterix leucopareia* (Van Someren, 1956). Van Someren claimed that both sexes incubated about equally in *E. leucopareia.* I found this to be broadly true of both *E. verticalis* and *E. australis* with the males doing slightly more incubation than the females, particularly in *E. verticalis* during the afternoon hours (Table 3).

Although I have shown (Maclean, 1968) that lark egg coloration tends to match the substrate, the eggs are not especially cryptic. Crypsis is conferred upon the nest and eggs by the parent bird itself, whether it covers the whole nest cup as in *Alauda starki* (fig. 4) or sits deeply in a relatively larger nest cup as in *Spizocorys conirostris* (fig. 5). Associated with this is the fact that all the sandveld larks sit very closely when incubating, unless disturbed by a human intruder on foot, in which case most larks leave the nest while the intruder is still some distance from the nest. This is especially true of the *Mirafra* species and of *Chersomanes albofasciata.*

The male of *Eremopterix australis* commonly chases the female off the nest at the approach of danger; he does this by flying over the territory and diving suddenly down to the nest, causing the female to depart precipitately.

The incubation period in all the sandveld larks (except for *Mirafra sabota* and *M. apiata* for which I have no data) is 12 days, with a minimum of 11 days and a maximum of 13 days. This is within the range of lark incubation times recorded in the literature: 11 or 12 days (Hartley, 1946; Kendeigh, 1952; Lovell, 1944) and 10 to 12 days (DuBois, 1935, 1936). The long incubation period of 14 days for *Calandrella cinerea* recorded by Winterbottom & Wilson (1959) is probably based on inadequate data, as these workers themselves imply.

TABLE 2

Species	Egg measurements (mm)													
	Length							Diameter						
	Summer			Winter				Summer			Winter			
	Mean	N	S.E.	Mean	N	S.E.	p	Mean	N	S.E.	Mean	N	S.E.	p
E. verticalis ..	19·1	109	0·0634	19·4	158	0·0664	<0·01	13·7	109	0·0366	14·0	158	0·0403	<0·01
E. australis	18·3	52	0·1182	18·3	49	0·1174	>0·50	13·3	52	0·0726	13·6	49	0·0586	>0·50
C. albofasciata ..	20·7	27	0·165	20·9	37	0·158	>0·50	14·8	27	0·0718	15·0	37	0·0891	>0·95

Differences between summer (October to March) and winter (April to September) egg measurements in *Eremopterix verticalis*, *E. australis* and *Chersomanes albofasciata* in the Kalahari sandveld. Only in the case of *E. verticalis* is the difference statistically significant. N = sample number. S.E. = standard error. p = probability.

TABLE 3

E. verticalis								*E. australis*							
Morning				Afternoon				Morning				Afternoon			
♂	♀	Total	% ♂	♂	♀	Total	% ♂	♂	♀	Total	% ♂	♂	♀	Total	% ♂
47	44	91	51·6	70	44	114	61·4	38	31	69	55·1	8	7	15	53·3

Number of observations of incubating male and female *Eremopterix* in the morning (before 1200 hours) and afternoon (after 1200 hours), showing the percentage of incubation done by the males.

NESTLING PERIOD

After hatching there is no trace of egg shells left in the nest. Probably they are carried away by the parents. In all species both parents feed the young (figs. 8, 9, 10, 11 and 13) and in the two *Eremopterix* species and in *Alauda starki* both parents brood the young (figs. 6 and 7). The male appears to brood only about one-third as much as the female in *Eremopterix verticalis*; the male *E. australis* on the other hand seems to do most of the brooding (Table 4). The figures in Table 4 can be taken only as the most general indication of the situation in these larks because the number of observations in each species is rather small.

Except for *Alauda starki* which feeds its young to a large extent on green grass seeds, the sandveld larks feed their young almost exclusively on insects and their larvae. One of the commonest insects given to the young is the harvester termite *Hodotermes mossambica* (fig. 9), but grasshoppers (fig. 10) and lepidopterous larvae are also common food items in all species.

Each species of lark has a characteristic feeding call which releases begging in the chicks (figs. 8, 10, 11, 13, 15, 16 and 17). The parental feeding call of *Chersomanes albofasciata* is similar to the flight call, but quieter. The feeding calls of the *Eremopterix* species are similar in their trilling quality, but in *E. verticalis* the note is a faint double 'tsee-ree', while in *E. australis* it is a single short 'preep'. The feeding call of *Alauda starki* is also a double note, a quiet 'chop-chop'. Very young chicks of all species can be made to beg in response to a soft, high-pitched whistle, but once their eyes are open they crouch flat in the nest and cease to respond by begging, except of course to the parental calls.

TABLE 4

E. verticalis								*E. australis*							
Morning				Afternoon				Morning				Afternoon			
♂	♀	Total	% ♂	♂	♀	Total	% ♂	♂	♀	Total	% ♂	♂	♀	Total	% ♂
6	13	19	31·6	6	11	17	35·3	7	3	10	70	3	1	4	75

Brooding of young in *Eremopterix*, showing the number of observations for both sexes in the morning (before 1200 hours) and in the afternoon (after 1200 hours), and the percentage of brooding done by the males.

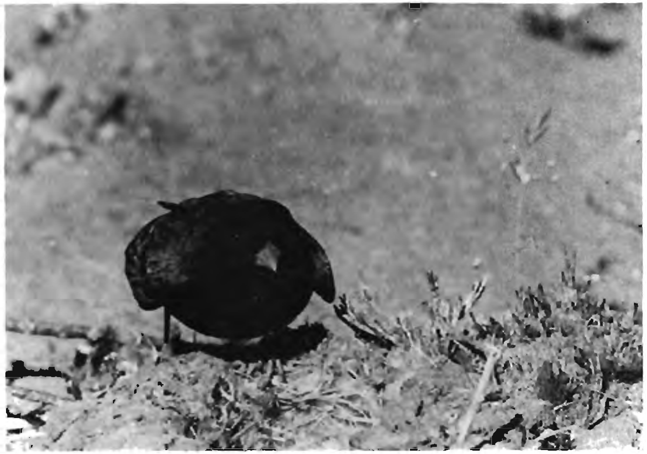

Fig. 3. A male *Eremopterix australis* about to incubate.

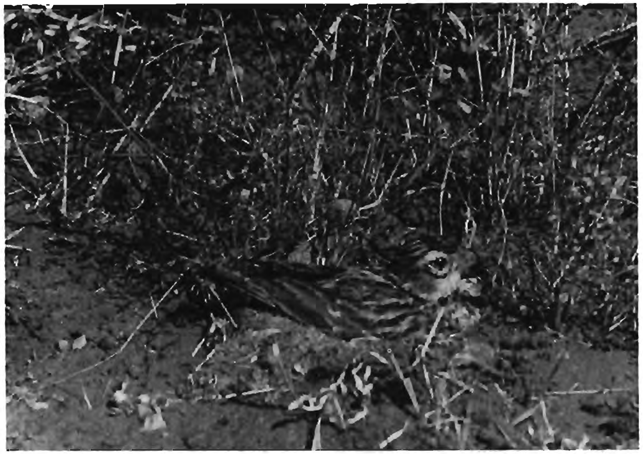

Fig. 4. *Alauda starki* incubating. The extreme crypsis of the sitting bird is well illustrated.

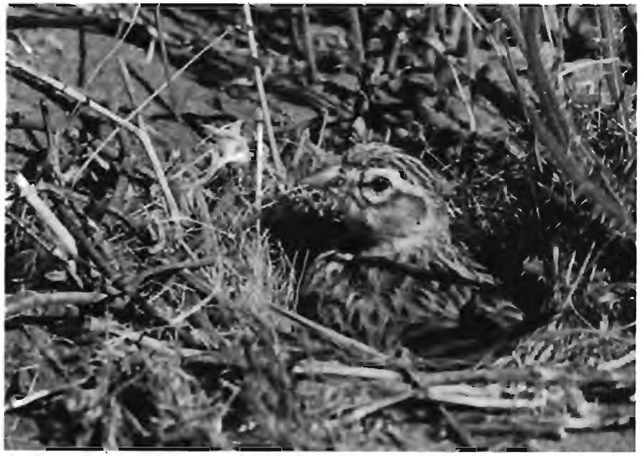

Fig. 5. *Spizocorys conirostris* incubating. Note the relatively large nest cup into which the whole bird fits.

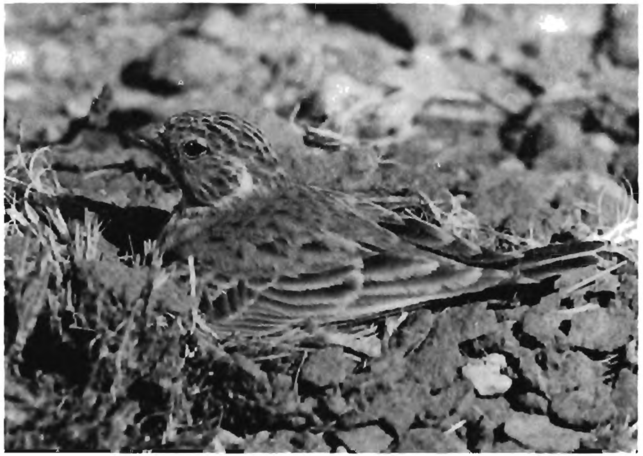

Fig. 6. A female *Eremopterix verticalis* brooding small chicks.

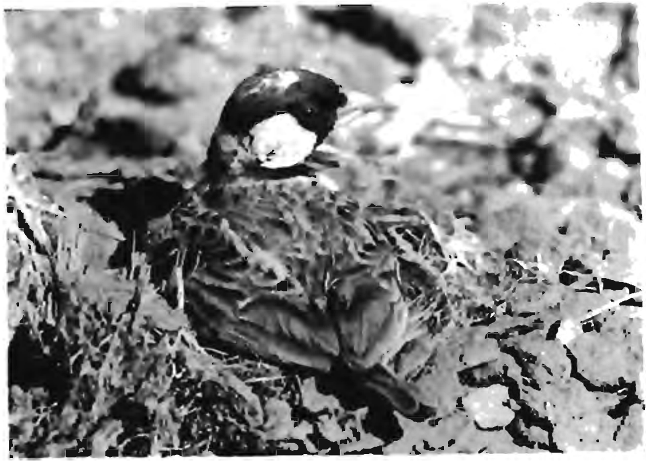

Fig. 7. A male *Eremopterix verticalis* brooding small chicks.

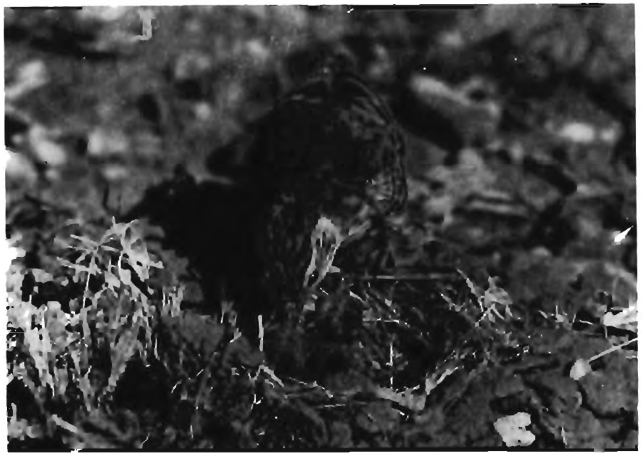

Fig. 8. A female *Eremopterix verticalis* feeding chicks.

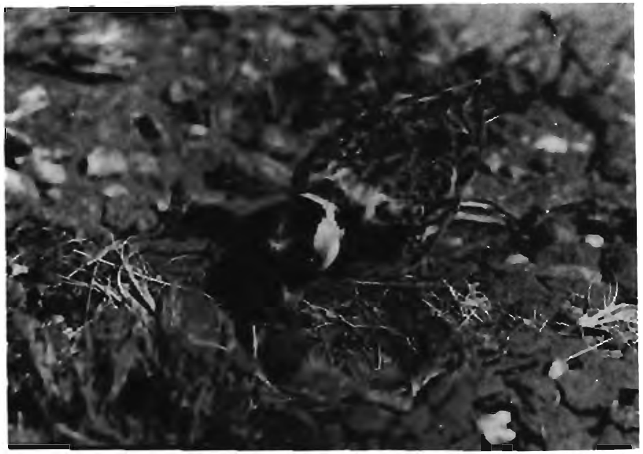

Fig. 9. A male *Eremopterix verticalis* feeds *Hodotermes mossambica* to a small chick.

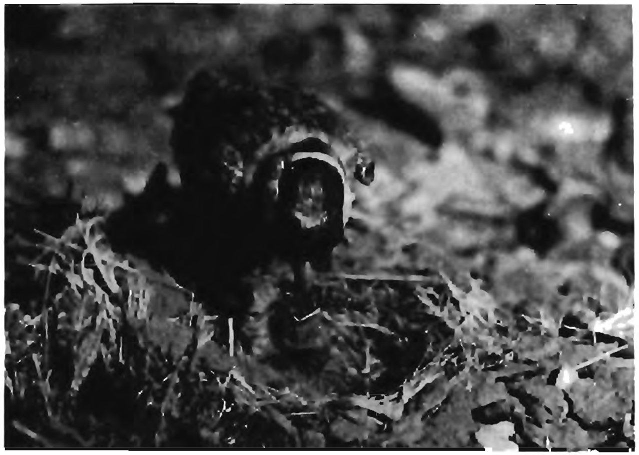

Fig. 10. A male *Eremopterix verticalis* feeds the abdomen of a large grasshopper to a small chick, which swallowed it after two attempts; if a chick of this size cannot swallow the food, the parent will eat it instead.

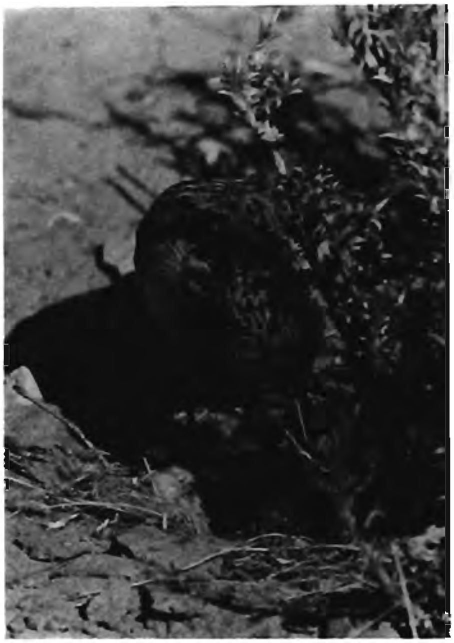

Fig. 11. *Chersomanes albofasciata* feeding a chick: note how deeply the parent's bill is inserted into the chick's throat.

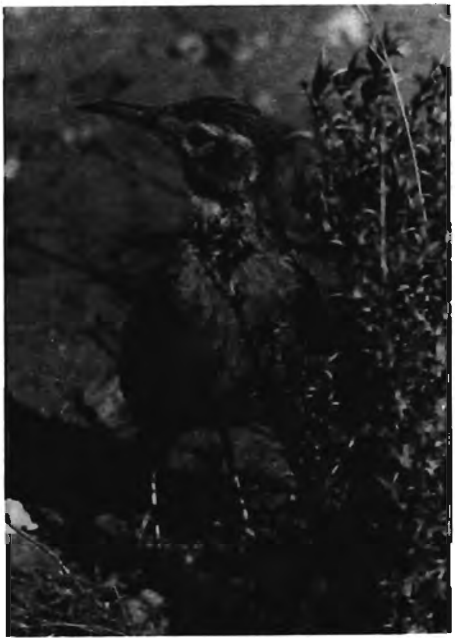

Fig. 12. Having just fed, a *Chersomanes albofasciata* waits for the chick to defaecate.

Nest sanitation is performed by both sexes. After feeding a chick, the parent will wait at the nest (fig. 12) until the chick deposits a faecal sac on the nest rim. The parent carries the sac in its bill to a distance of three or four metres and drops it on the ground; it then wipes its bill on any convenient stone.

Once they begin to fledge, chicks of all species of larks react to an intruder by crouching in the nest. If approached too closely, they raise the crown feathers and maybe even the back feathers. At all ages the chicks react to insects crawling over them by vigorous body-shaking; this usually effectively removes the insect or at least causes it to run away.

In all species the chicks grow rapidly and are almost fully fledged dorsally within six days. Young *Eremopterix verticalis* may leave the nest at the age of seven days, but the usual nestling period for all species was ten days. The longest nestling period of 14 days occurred in one case of *Mirafra africanoides*. Other published records of lark nestling periods are shown in Table 5.

It appears that young fledged larks do not leave the nest voluntarily, but are led away by the parents. A potentially dangerous situation near a nest will cause a parent bird to lead a chick from the nest at an age when it is barely able to walk. I have witnessed departure from the nest by the chicks of *Chersomanes albofasciata* and the two *Eremopterix* species.

In the case of *Chersomanes albofasciata* the chick was about ten days old when one of the parents began to call to the chick from a distance of one or two metres from the nest. The chick grew restless and moved about in the nest before tottering feebly about 30 to

TABLE 5

Species	Nestling period (days)			Reference
	Min.	Normal	Max.	
Mirafra javanica		10		Bourke (1947)
Galerida cristata	8	10	11	Hartley (1946)
Eremophila alpestris	9		12	DuBois (1935)
,, ,,		12		Lovell (1944)
,, ,,	9	10–11	14	Pickwell (1931)
Eremopterix leucopareia		14–15		Van Someren (1956)
Calandrella cinerea		10–12		McLachlan & Liversidge (1957)
,, ,,		16–17		Van Someren (1956)
,, ,,	9	12	18	Winterbottom & Wilson (1959)

Nestling periods of various species of larks in the literature.

40 cm from the nest. It then returned to the nest for about ten minutes before the parent finally managed to call it out again. The chick was last seen following the parent slowly away from the nest. The parental call was probably the equivalent of the feeding call.

Once I came across a female *Eremopterix verticalis* which had lured a chick from the nest to a distance of just under a metre. The female gave the alarm call, at which the chick ran back to the nest where it crouched until I approached it on foot. At that it left the nest again uttering the 'chireep' distress call as it ran.

The sequence of events in chick-departure was more fully seen in *E. australis*. On 14 July a nest contained two chicks between seven and nine days old; both parents were feeding them (fig. 13). The female was much concerned by the proximity of the motor vehicle and began to call the chicks with the 'preep' feeding call. One of the chicks reacted by trying to leave the nest (fig. 14), which it eventually succeeded in doing. It sat next to the nest as the female returned to fetch the second chick (fig. 15). However, the second chick merely begged and made no attempt to depart (fig. 16). The male bird returned with food and after feeding the first chick, he stood by as the female continued in her attempts to get the chicks to follow her (fig. 17). Since the second chick was clearly unable to do so, I replaced the first one in the nest and left. The second chick was found about 25 cm from the nest on 18 July, four days later.

Once the lark chicks have successfully left the nest, they behave much as the chicks of precocial non-passerine birds. They crouch when alarmed (figs. 18 and 19), but can run quite well when pursued. I could not determine the exact age at which the chicks could fly, but those that left the nest at the age of ten days could probably not fly for another week or so. I estimate the flying age of young larks to be between 15 and 20 days, but my evidence is entirely circumstantial.

INTRUDER REACTIONS OF NESTING LARKS

1. *Mirafra africanoides*

Fawn-coloured Larks are usually undemonstrative during the incubation period. When flushed from the eggs, the bird simply disappears into the grass and remains invisible as long as the intruder is at the nest.

When the birds have young, however, their behaviour at the nest is quite different. Both parents utter a whistled 'peeek' alarm note that sounds almost identical to the alarm call of the Ant-eating Chat *Myrmecocichla formicivora.* This note may be uttered from the ground or from a perch on a bush or tree. It may also be given during the alarm flight in which the birds flutter about with a sort of 'butterfly' flight. The alarm notes may be interspersed with bursts of true song in both sexes. *Mirafra africanoides* appears not to indulge in injury-feigning distraction displays in the sandveld.

2. *Mirafra sabota*

A very thin, high-pitched 'si si si' is the alarm note of the Sabota Lark near the nest. Under similar circumstances these larks also utter a perfect imitation of the 'piiiííí' anxiety call of the Double-banded Courser *Rhinoptilus africanus*; this may be an example of imitation in which the context of the imitated call has been retained.

3. *Mirafra apiata*

Although I found no nests of the Clapper Lark in the sandveld, I saw displays which could be interpreted only as distraction and alarm displays. Whether the birds had eggs or young was of course not determined. Both sexes perform a bouncing 'flip-flip' flight in which the wings are sharply snapped at each flip, at about one-second intervals. Now and then the displaying birds land, only to jump up immediately and continue the snapping display flight.

One member of a pair, probably the male, was heard uttering a variety of notes while perched on top of a small tree. The first of these notes was a repeated 'peeek' exactly like the alarm note of *M. africanoides* and probably having a corresponding function. This note was sometimes drawn out until it almost resembled the true song whistle. Another alarm note was a grating 'chrk-chrk'. A third type of note consisted of a trilling 'prrr peeu', much like the call of *Chersomanes albofasciata*; it possibly constituted imitation, but the function of the note was not determined. At times the 'chrk-chrk' and 'prrr peeu' notes were interspersed so as almost to form a song, but the situation was clearly one of alarm.

4. *Chersomanes albofasciata*

The Spike-heeled Lark usually gives a few 'prrr-prrr' flight notes after being disturbed at the nest, whether with eggs or young, but occasional individuals indulge in a spectacular distraction display. One tame parent bird approached to within one metre of me as I was measuring its eggs and then did a rodent-run display away from me; as it ran it fluffed up the back and breast feathers, fanned and depressed the tail and drew the head in towards the body. The effect of the fanned tail with its black-and-white pattern was striking (fig. 20). The display was enhanced by a series of loud notes which I transcribed as 'chip kwip kwip kwip ti ti ti ti ti ti chirri chirri chirri'.

When I moved to 1·5 metres from the nest, the bird returned and settled down to incubate, uttering soft 'chirri chirri' notes. When approached again, it shuffled off the nest and repeated the distraction display, this time partly spreading the wings.

At another nest containing two chicks, the agitated parents uttered alarm calls during a bouncing flight just a couple of metres above the ground; this was in response to a Cape Cobra, *Naja nivea*, that was approaching the nest.

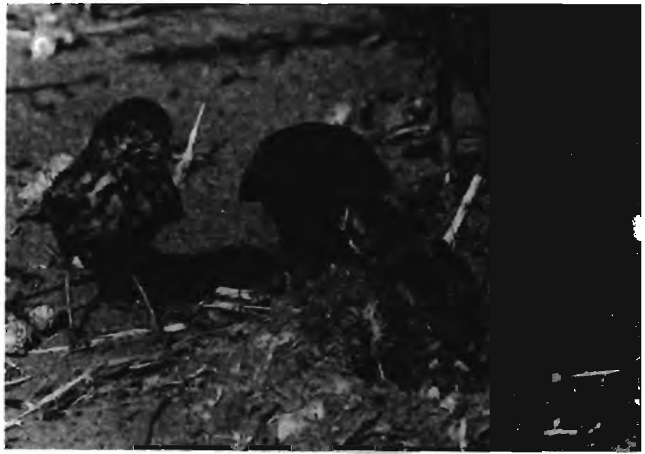

Fig. 13. A male *Eremopterix australis* feeds a chick as the female stands anxiously by; her anxiety is shown by the depressed plumage.

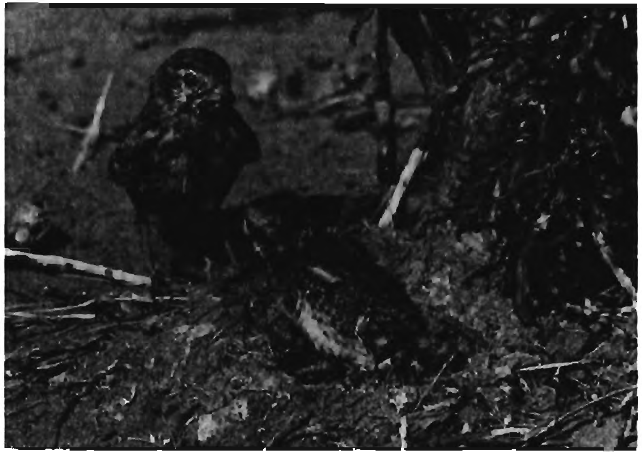

Fig. 14. A female *Eremopterix australis* calling her chicks out of the nest. The chicks are about 8 days old.

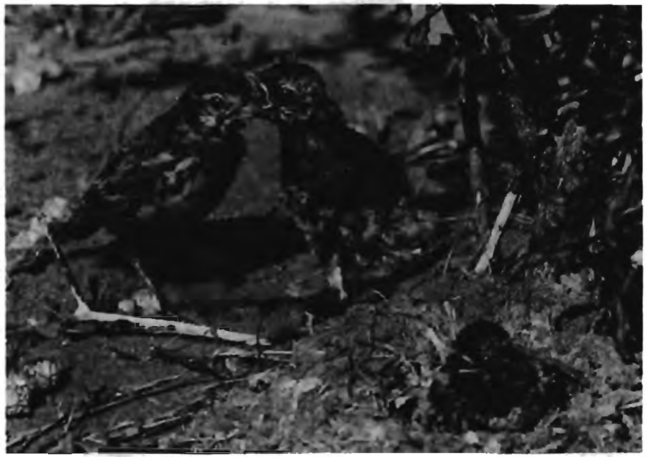

Fig. 15. Having successfully called one chick from the nest, the female *Eremopterix australis* returns to fetch the second chick.

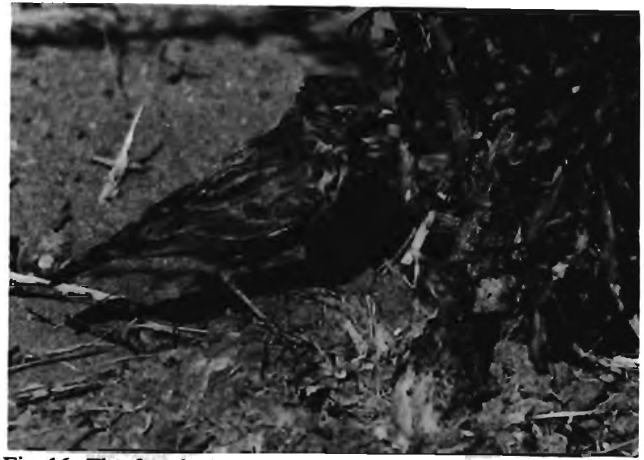

Fig. 16. The female *Eremopterix australis* calls the second chick which responds by begging. The first chick is hidden by the female.

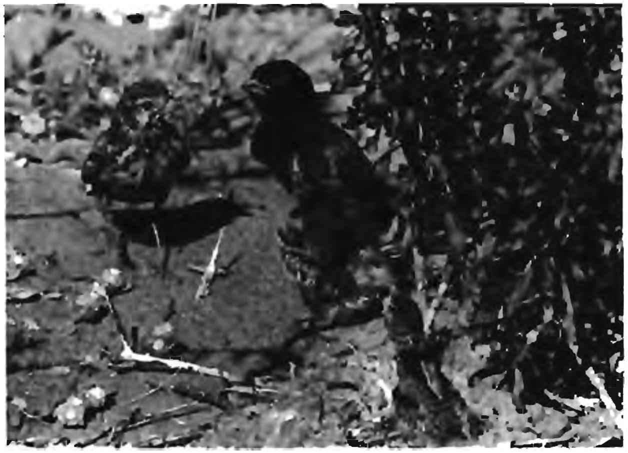

Fig. 17. The male *Eremopterix australis* stands by as the female runs to and from the nest in an attempt to get the second chick to leave the nest; the first chick is preparing to follow the parents, while the second chick just continues to beg at increasingly higher intensity.

Fig. 18. A fledging *Chersomanes albofasciata* chick that has recently left the nest.

Fig. 19. An almost fully fledged *Alauda starki* chick, several days out of the nest, but able to fly only a metre or less at a time.

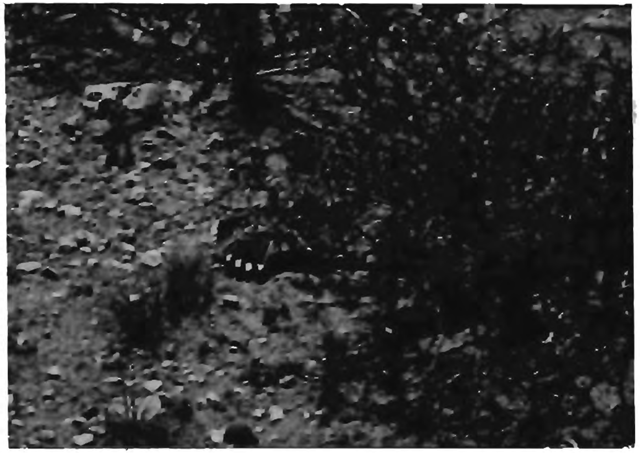

Fig. 20. The distraction display of *Chersomanes albofasciata* near its nest with eggs. The bold tail pattern stands out well, while the cryptically coloured body plumage merges in with the background.

On another occasion a group of five *Chersomanes albofasciata* (possibly non-breeding birds) gave a combined alarm display at the entrance to a burrow into which a cobra had just disappeared. The birds all stood around with bodies upright, necks stretched, wings open and tails fanned. They accompanied this posturing with harsh 'cheee' notes. Now and then a bird would jump away from the burrow and return immediately to repeat the display.

5. *Eremopterix verticalis*

When flushed from the nest, whether with eggs or young, the Grey-backed Finch-lark is usually rather undemonstrative. It does, however, have a characteristic, if simple, alarm note—a single 'prink' differing little from the flight call.

Males occasionally perform a flight display in which they swoop low over the ground with wings held at a high dihedral. This may be a type of distraction display, or it may serve to chase a female from a nest, although I have not seen this happen. There is a stronger likelihood that this display is connected with pair formation or territoriality, as it is done only by the males.

An incubating bird that has been kept from its nest for several minutes sometimes returns to perform a bouncing flight directly over the nest, as in *Spizocorys conirostris*. This may serve as a distraction display.

6. *Eremopterix australis*

The Black Finch-lark indulges in frequent and elaborate distraction displays near the nest, whether with eggs or young, in marked contrast to the placid *E. verticalis*. Male *E. australis* are particularly given to these displays.

The first type of distraction display is a 'butterfly' flight over the territory; a variation of this is fluttering and hovering over the nest. I have seen this display performed only by males. It is accompanied by a buzzing 'dzee' alarm note and a 'preep' note hardly distinguishable from the flight call of *E. verticalis*. Sometimes a male *E. australis* perches on top of a shrub and postures exaggeratedly with spread wings before resuming the butterfly flight, which may end in a sudden dive into the shrubs.

The second distraction display is of the injury-feigning type and is performed by both sexes. The birds fly towards the intruder with loud wing-beats (in the males this sound is a high-pitched 'whoop'), flop down on the ground and then flutter away along the ground with a raspy 'chee-chee-chee-chee' distress call in the female; the corresponding call in the male is a soft 'tik tik tik tik'.

One further alarm reaction in one male *E. australis* consisted of a display flight with wing snaps at half-second intervals. This male had a fledged chick near by, but the species is highly demonstrative even when there are freshly laid eggs in the nest.

7. *Spizocorys conirostris*

When flushed from a nest with eggs, the Pink-billed Lark often bounces in the air above the nest for a few seconds before departing. As it does so, it utters the three- or four-syllable 'tri-tri-tri' flight call. A less common reaction is a rapid departure from the nest followed by a fluttering flight low over the ground for several metres; this may be followed by a return of the bird in normal flight to the nest as it utters the alarm call, a high '*see*-si-si' repeated at frequent intervals.

A group of 11 adult *S. conirostris* was once seen mobbing a Black-backed Jackal, *Canis mesomelas*, which had ventured into the birds' breeding area.

8. *Alauda starki*

The simplest alarm reaction of Stark's Lark is crest-raising. The crest is seldom raised, however, when the bird is right at the nest. A display flight that may serve as a distraction display resembles very closely a similar display exhibited by the two *Eremopterix* species. In its simplest form this display consists merely in the birds flying up to a few metres uttering the 'tree' flight call and then coming down to the ground again, repeating this up-and-down flight as long as necessary. A more highly-developed form of the display consists of a 'flip-flip' bouncing flight in the air, followed by a sudden dive with wings held partly folded at a high dihedral. The flip-flip flight may be enhanced by clearly audible wing-snapping in short bursts, giving a loud 'prrp prrp' sound.

Alauda starki also has a well-developed injury-feigning display in response to distress calls from fledged young. The display is exactly like the one described for *Eremopterix australis* and is accompanied by a soft 'zzz' note as the birds flutter along the ground.

GREETING DISPLAYS BY MALE TO FEMALE

Throughout the breeding cycle up to and including the time the young leave the nest, the males of both *Eremopterix* species and of *Chersomanes albofasciata* frequently display briefly to their mates whenever they encounter each other at the nest.

The greeting note of *Eremopterix australis* is a trilled 'preee' which may or may not be accompanied by the head-up, tail-up greeting display (fig. 21B). This display is quite different from the threat display of this genus, in which the head and tail are down (fig. 21A). The greeting posture of *Chersomanes albofasciata* includes raising the tail and drooping the wings, but the head is not noticeably raised; it is only an assumption that the male performs this display, as I have never seen it in female *Eremopterix*, but this needs verification.

Other sandveld larks probably also have such greeting displays, but I have not had the opportunity to observe them.

DISCUSSION

The functions of song-flights in the larks are obvious; they are a group of terrestrial birds that are otherwise difficult to see. A parallel situation occurs in the pipits (Motacillidae). The taxonomic significance of these song flights has already been discussed (Maclean, 1969). Although female *Mirafra africanoides* sing as well as the males, no song has been recorded for the females of the sexually dichromatic *Eremopterix* species. The social organization of *Eremopterix* is such that the sexes are always together, either as pairs during a breeding season, or in mixed flocks at other times. There is no territoriality when the birds are not breeding and therefore no song. Song is evident only when the males are establishing territories prior to breeding after the rains when conditions are suitable.

The situation in the other nomadic species of sandveld larks, *Spizocorys conirostris* and *Alauda starki*, is not so easy to assess because of the similarity of the sexes, but the same arguments almost certainly apply to them as to the *Eremopterix* species. But the case of *Mirafra* is quite different. All three *Mirafra* species can be heard singing throughout the year, regardless of conditions. It is therefore probable that these non-nomadic, non-

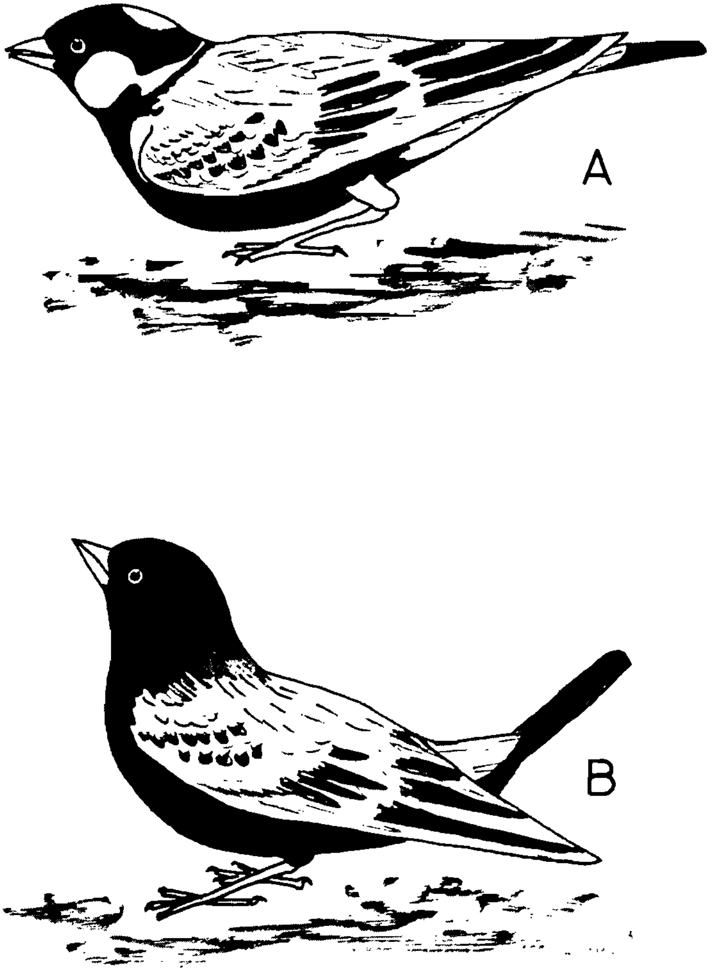

Fig. 21. A. The threat display of the male *Eremopterix verticalis*.
B. The greeting display of the male *E. australis* as he meets the female at the nest.

gregarious larks are territorial at all times and it is equally probable that the females also establish territories when they are not breeding, much as do female Robins, *Erithacus rubecula* (Lack, 1953). We know nothing of the social organization of the *Mirafra* larks outside of the breeding season, except that they do not form flocks, so it is not possible to say whether or not the pair is a permanent social unit, or if it is formed for only a single breeding season. The latter alternative is the more likely, as it applies to most small passerines, hence the development of song in the females.

The roles of the sexes in other aspects of lark breeding biology are of considerable importance. The rule throughout the Alaudidae is, as I have shown, that the female is the sole nest-builder. Why it should be the role of the male *Eremopterix australis* to bring the sandy spider web to decorate the nest is not at all clear, especially since he makes no attempt to build with it and also since he brings no other sort of nest material. How such a behaviour pattern could have evolved is a matter of pure conjecture at this stage. Belcher (1958) described a nest of *E. australis* near Victoria West as having 'what looked like a plastering of muddy earth' on the rim; this was more than likely the sandy spider web mixture that I recorded in the Kalahari. One further example suggests that this type of nest decoration is more widespread among the larks than at present seems to be the case: Norris (1964) described the nest of the Bifasciated Lark *Alaemon* (= *Certhilauda*) *alaudipes* as lined with woolly material coated with sand that was 'well smoothed (or possibly plastered)'.

The trend in some lark species is toward incubation by the female only (Abs, 1963; DuBois, 1935; Hartley, 1946; Forbush, 1927), but in most species both sexes incubate. It seems strange therefore that more incubation is done by the male bird in those species (e.g. *Eremopterix*) in which sexual dichromatism is most marked, with the accent on conspicuously coloured aggressive males. Belcher (1958) states that he never put the female of *Eremopterix australis* off the nest—only the male.

The brooding pattern of *E. verticalis* would seem to be more 'normal' in view of the sexual differences, but the increased parental role of the male *E. australis* is even more marked after hatching than during incubation. Data are needed on the respective feeding rates of the young by the two sexes in all the sandveld larks. Although both sexes feed the young in all lark species so far studied (DuBois, 1936; Hartley, 1946; Van Someren, 1956; Wadewitz, 1957), their relative roles have not been well documented.

More information is also needed on regurgitation as a feeding mechanism in larks. I have seen *Alauda starki* carrying seeds inside the bill and, in view of the note by Steyn (1964) on the regurgitation of seeds by a female Chestnut-backed Finch-lark *Eremopterix leucotis*, it is possible that Stark's Lark also regurgitates seeds. Insects are carried in the bill and, since I have not seen either *E. verticalis* or *E. australis* feeding their young on anything but insects, it is not possible to say whether or not they regurgitate food at any time.

The task of leading the young from the nest appears always to fall to the female. This is true of both the sandveld species of *Eremopterix* and has been noted also for *E. leucotis* (Steyn, 1964) and for *Eremophila alpestris* (Pickwell, 1931). It probably applies to other larks too, although it is dangerous to generalize about the parental roles of the sexes in this family of birds in view of the differences between one species and another that have already been mentioned in connection with incubation.

The size differences between winter and summer eggs of *Eremopterix verticalis* constitute a curious phenomenon, especially since these differences are not evident in either *E. australis* or *Chersomanes albofasciata*. The suggestion exists that the difference is a function of differences in temperature, but why are the other two species not similarly affected?

An alternative suggestion is that the summer and winter breeding populations of *Eremopterix verticalis* came from different areas and might be subspecifically distinct. No specimens of either population were collected, but it is not all impossible that at least two subspecies, *E. v. verticalis* and *E. v. damarensis*, occur in south-western Botswana and the Gemsbok Park from time to time (White, 1961; Smithers, 1964). Benson & Irwin (1965) indicate that these two subspecies and at least one other, *E. v. khama*, breed in Botswana, while the former two also occur together sometimes in Rhodesia. Since the species is highly nomadic and since there was an almost total exodus of *E. verticalis* from the Gemsbok Park between the winter breeding season of 1965 and the summer breeding season early in 1966 (Maclean, in press), the two populations could well have come from different areas. Moreover, since there is only one geographical form of *E. australis*, there would have been no noticeable difference in egg size between the winter and summer populations, unless egg size had been determined by ambient temperature or some associated factors.

A similar argument may be said to apply to *Chersomanes albofasciata*, which is a resident species; the summer and winter eggs would therefore in effect have been samples from the same population, hence the absence of a significant size difference. The argument can be resolved only by making further measurements of eggs in different seasons, combined with systematic collecting of breeding birds.

Distraction displays in larks are probably widespread but poorly documented. Injury-feigning in *Eremophila alpestris* is often mentioned (DuBois, 1936; Forbush, 1927; Hartley, 1946; Pickwell, 1931). Bannerman & Priestly (1952) describe a high-intensity threat display in *Alaemon alaudipes*, in which the bird left its nest and ran at the intruders with its wings spread and beak open. This display sounds similar to the open-wing display of *Chersomanes albofasciata*. On the whole, however, lark distraction displays are not especially distinctive when compared with corresponding displays in other bird groups.

I have said very little about courtship postures and other intersexual behaviour in the larks of the sandveld because the incidental nature of this study did not provide a sufficiently thorough set of observations which might allow of adequate interpretation. A glance at fig. 21 shows, however, that in the threat posture, the bird is positioned ready to spring forward at its opponent with the bill directed for attack; the greeting posture on the other hand is completely non-aggressive, and serves instead to present to the female the striking black underparts of the male. Perhaps the lack of distinctive ventral plumage patterns in the male *Chersomanes albofasciata* makes redundant the raising of the head in the greeting posture of this species, but the raised tail displays a conspicuous pattern.

SUMMARY

Eight breeding species of larks were studied over a 19-month period in the Kalahari Gemsbok National Park. Their songs and song-flights are described. Only the female builds the nest in the genus *Eremopterix* and probably in all the other species too. Nests take from four to seven days to complete.

Summer eggs of *Eremopterix verticalis* are significantly smaller than winter eggs; this difference is not significant in either *E. australis* or *Chersomanes albofasciata*, so the summer and winter populations of *Eremopterix verticalis* might have been two different subspecies.

Both sexes incubate the eggs in *Eremopterix*, the males doing slightly more than the females. Both sexes brood the chicks in *Eremopterix* and in *Alauda starki*. In *Eremopterix verticalis* the female does most of the brooding; the reverse applies in *E. australis*. Both sexes feed the chicks in all species. Chicks of all species leave the nest at about ten days; they are led away by the female.

Intruder reactions in the form of distraction and alarm displays and calls are described, as well as greeting displays of males to females.

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